

Habitat Association and Distribution of *Nauticaris marionis* at the Sub-Antarctic Prince Edward Islands

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Abstract

The habitat associations between the caridean shrimp *Nauticaris marionis* and sessile epibenthic assemblages and substratum types of the Sub-Antarctic Prince Edward Islands were investigated. Twenty five stations, varying in substratum type, depth and location on the shelf and slope around the islands were sampled photographically with a towed benthic camera sled. At each station the substratum type was classified, sessile epibenthic cover was quantified through the use of digital quadrats and shrimp density was estimated. Results add to the broadly described distribution patterns of *N. marionis* by identifying specifically the habitat characteristics they generally utilize. The distribution of *N. marionis* was found to be influenced by a combination of substratum and sessile epibenthic assemblages, but not substratum type alone. Shrimp inhabited stations with >50 % biogenic cover on mud and gravel substrata, but were not found at stations with rocky-sand or rocky-mud substrata. Their distribution appears to also be influenced by depth, as shrimp were only found within a depth range of 50 - 160 m in this study. A strong correlation was found between *N. marionis* density and depth. Shrimp were found both inshore around the islands, and on the relatively shallow saddle between the islands. In comparison with previous studies, *N. marionis* was found at similar, if not higher, densities in this study, although they occupied a narrower depth range.

1. Literature Review

Habitat associations

Habitat associations between species in the marine environment are well documented around the globe. Sessile organisms creating structures such as coral reefs, mangrove trees and kelp forests provide mobile animals with structural habitat complexity, relief from physical stresses, increased surfaces for further macrophytic or epibenthic colonization, and often provide a source of food. While megafaunal invertebrates may enhance the structural complexity of fish habitat, they also contribute to biodiversity, play important ecological roles and can be indicators of long-term environmental conditions (Brusca and Brusca, 1990; Puniwai, 2002, cited in Tissot *et al.* 2006). However, structures don't always need to be large in size to provide these benefits. Small-scale habitat complexity, including that caused by biogenic structures, has been shown to be important in structuring benthic communities and hence increasing biodiversity in an area (Bradshaw *et al.* 2003). At the smaller scale, habitat associations are known between several shrimp species and seagrass meadows (Coen *et al.* 1981), with dense stands hosting significantly more abundant aggregations of these crustaceans than bare stands in the northern Gulf of Mexico (Lewis, 1984). Some chitons will seek out canopy-forming algae, which provides shade and helps prevent desiccation (Burnaford, 2004). Certain species of polychaete worms have been found to congregate on bryozoan filter feeders (Sellheim *et al.* 2009). Not only does upright sessile epibenthos provide complex habitat for small invertebrates (Collie *et al.* 1997), but it may also play an important role as settlement substratum for juvenile invertebrates (Bradshaw *et al.* 2003). The development of sessile epibenthic assemblages on hard substrata have been extensively studied in tropical and temperate latitudes, however, research in high latitudes has only recently been conducted (Bowden *et al.* 2006). In the frigid waters of the Antarctic Circle, water temperature plays an important role limiting the colonisation and growth rates of epibenthic species which are, as a result, much slower than in temperate and tropical waters (Bowden *et al.* 2006). Because the benthos at these high latitudes is slow growing novel ways are needed to sample these often-pristine areas in order to keep disturbance to a minimum.

Techniques

Historical benthic sampling techniques have typically involved the use of dredges, grabs and benthic trawls. These methods can be very destructive to benthic communities, leading to a decline in biodiversity and even functional extinction as many ecological functions are performed by organisms sensitive to disturbance (Thrush and Dayton, 2002). Alternatives to conventional trawl samples have recently become more common place. Benthic tows using camera footage provide a minimal-disturbance alternative to benthic trawls that collect sessile and mobile fauna in a destructive manner, not in line with many conservation policies (Sheehan *et al.* 2010), and often losing valuable contextual information as a result of the sampling process (Solan *et al.* 2003). While it is sometimes difficult to identify specimens to species level using underwater photographs, this method adds value by way of providing visual information on densities and spatial distributions of benthic organisms (Rice *et al.* 1979). Density estimates tend to be higher in photographic surveys compared with trawls, grabs and dredges, as catch avoidance of mobile species can occur and the efficiency of collecting gear is inconsistent with different trawl gear configurations (Caillet *et al.* 1999). However, the surface area of the sea-bed in a single image, or even combined images, from a single transect is usually relatively small, so reliable data are mostly obtained only for abundant species (Rice *et al.* 1979). Nevertheless, benthic towed image analysis has proven to be an effective technique for use in a wide range of studies. Such studies include monitoring long-term change in deep benthic communities (Bailey *et al.* 2006), estimating disease prevalence on coral reefs (Francini-Filho *et al.* 2008), deep sea biomass surveys in submarine canyons (De Leo *et al.* 2010), examining the abundance and dispersion of epibenthic megafauna at abyssal depths (Lauerman *et al.* 1994), and abundance estimates of rocky shore invertebrates (Pech *et al.* 2004). Recent advancements in this method have been the development of stereo-video systems, which use paired cameras to allow accurate measurements of underwater objects. Stereo-video systems have so far been used for work on benthic community structure in coral reefs (Turner *et al.* 2015), and for determination of fish community structure, abundance and biomass (Santana-Garcon *et al.* 2014).

The Prince Edward Islands

The Prince Edward Islands are located in the Indian sector of the Southern Ocean approximately 1,900 km south-east of Cape Town (Figure 1). The two islands consist of the larger Marion Island (270 km²) and smaller Prince Edward Island (45 km²), which lies to the north-east of Marion Island. The islands are separated by 19 km of shallow inter-island coastal shelf, which reaches approximately 200 m in depth.



Figure 1. Map of the Prince Edward Islands and its position in relation to South Africa and Antarctica. Source: <http://scitechdaily.com/warming-ocean-temperatures-may-reduce-the-survival-rate-of-elephant-seals/>

In 2013 the Prince Edward Islands were proclaimed South Africa's first offshore marine protected area with the objective, amongst others, of reducing the impact of fishing activity on the native seabird populations (Lombard *et al.* 2007). Since 1995, the islands had been managed as a Special Nature Reserve, however, this status was only afforded to the land masses, and not the surrounding marine environment (PEIMWP, 1996, cited in Lombard *et al.* 2007). In an effort to reduce the seabird bycatch and to allow stocks of the Patagonian toothfish

(*Dissostichus eleginoides*) to recover, no fishing activity has been allowed within the 12 nautical mile territorial waters of the islands since December 2004.

Situated in the direct path of the Antarctic Circumpolar Ocean Current (ACC), between the Sub-Antarctic Front and the Antarctic Polar Front (Lutjeharms, 1985), the Prince Edward Islands share a host of similarities with other Sub-Antarctic islands, the nearest of which, is Crozet Island 950 km to the east. Southern Ocean islands, most of which are relatively young, volcanic islands, are best known for their high productivity, which supports an abundance of marine organisms and predatory land-based marine mammals and seabirds (Bergstrom and Chown, 1999). Yet, the relationships of the biota of the islands and their link to the southern continents have remained unknown. Although these islands may share monophyletic invertebrate taxa, their connection to similar fauna on the continents is poorly understood (Hall, 1990). The Prince Edward Islands also support large populations of seals and a variety of seabirds that utilize the islands during the breeding season (Ryan and Bester, 2008). It has previously been estimated that the islands support up to 5 million breeding pairs of predatory land-based marine animals during peak breeding season (Ryan and Bester, 2008).

A close terrestrial-marine interaction exists at the Prince Edward Islands, known as the islands' 'life support system' (Pakhomov *et al.* 2009). It is believed that as a result of this close interaction, the islands are able to accommodate large populations of predators and a rich marine benthic community. The high marine productivity experienced around the island, which drives this life support system and directly and indirectly provides food to the benthos and land-based predators, is thought to be the result of a combination of inshore (autochthonous) island dynamics, and an offshore (allochthonous) component. The inshore component is vital for a few predators, most notably southern rockhopper (*Eudyptes chrysocome*), eastern rockhopper (*Eudyptes filholi*) and macaroni penguins (*Eudyptes chrysolophus chrysolophus*) which hunt in close proximity to the islands and also plays an important role in seeding the rich benthos. However, it is the offshore component that

sustains the vast majority of predators (king penguins, petrels and albatrosses) on the islands including king penguins (*Aptenodytes patagonicus*), petrels and albatrosses (Pakhomov and Chown, 2003).

The inshore component of the 'life support system' is largely due to an island mass effect, by which the presence of the islands enhances their own biological ecosystem by influencing oceanographic processes around the islands. In the context of Prince Edward Islands this largely has two explanations: An upwelling hypothesis and a water-trapping hypothesis. Early oceanographic studies surrounding the Prince Edward Islands proposed that the upwelling of deep Antarctic waters on the lee side of islands was primarily responsible for the high productivity observed in this region (Grindley and Lane, 1979). Although this hypothesis was supported by the presence of cold, nutrient-rich water and high levels of productivity in the lee of the islands, it was ultimately dispelled due to low concentrations of silica found in surface waters, and the fact that upwelling was only described on one sampling cruise and not reconfirmed in any subsequent surveys (Allanson *et al.* 1985). Upwelling is usually associated with high nutrient concentrations, including silica, which is important in the production of diatoms (Chai *et al.* 2002).

The water-trapping hypothesis provides a more robust explanation for the high levels of productivity generated by an island-mass effect at the islands (Pakhomov *et al.* 2009). During periods when the SAF is located towards the north of the islands, advective forces are weakened, and eddies trapped on the Prince Edward Island inter-shelf saddle cause the water to be retained in this area for longer (Pakhomov *et al.* 2000). This, as well as increased stratification of the water column and nutrient run-off from the islands allows for the enhancement of primary productivity, and the proliferation of algal blooms (Perissinotto and Duncombe Rae, 1990).

The offshore component of the 'life support system' supports those predators that feed beyond the coastal shelf of the Prince Edward Islands. The easterly flowing ACC advects plankton and nekton-rich water from upstream

of the islands, which is then trapped between the islands by the shallow topography (Pakhomov and Froneman, 1999). The phytoplankton is then preyed on by visual zooplankton predators during the daytime. At night this food supply is then replenished from upstream advection. This is known as the 'replenishing hypothesis' (McQuaid and Froneman, 2008). Advection of allochthonous zooplankton has been postulated to supply the food resources necessary for feeding the bulk of the marine predators inhabiting the islands (Perissinotto and McQuaid, 1992). This production may be as much as two times the autochthonous algal production (Perissinotto and Boden, 1989). Although this meets the needs of zooplankton predators, predators feeding on myctophid fish and larger crustaceans are forced to forage in deeper waters, typically around the outside of the islands as these prey are able to avoid advection and instead can be found offshore around the islands, particularly on the lee side (Pakhomov and Froneman, 1999).

Recent studies have shown that the range of eddies located in the vicinity of the Prince Edward islands are not the product of current flow-through of the islands themselves, but instead originate much further upstream when the ACC crosses the Andrew Bain Fracture zone in the South-West Indian Ridge (Ansorge and Lutjeharms, 2003). There is, therefore, a train of eddies that continually traverses the Prince Edward Islands resulting in highly variable current speeds, current directions and water types. These eddies may carry unique zooplankton communities from their origins, and enhanced phytoplankton stocks, giving the islands a more diverse spectrum of biota than normally expected around an island in the sub-Antarctic (Pakhomov and Froneman, 1999). Many birds (Nel *et al.* 2001) and seals (Klages and Bester, 1998) from the islands have strong associations with these eddies when foraging, particularly upstream, where the biomass of micronekton and macroplankton is significantly higher than in the weaker eddies recorded closer to the islands (Ansorge and Lutjeharms, 2005). The train of eddies, therefore, contributes substantially to the offshore component of the Prince Edward Islands' life support system.

Even though the waters around the Prince Edward Islands experience higher productivity levels compared to the greater surrounding pelagic environment and phytoplankton blooms are a regular occurrence, it is widely accepted that this primary production is poorly utilized by planktonic herbivores (Perissinotto and Boden, 1989; Perissinotto, 1992). Instead, senescence transfers much of this energy to the sea floor, which enriches the benthos.

Nauticaris marionis

One of the few epibenthic organisms that is preyed on by land-based predators is the epibenthic shrimp, *Nauticaris marionis*. This makes it a key component of the system because it forms a trophic link between phytoplankton and top predators, indirectly making the plentiful primary production available to higher trophic organisms (Perissinotto and McQuaid, 1990). While gut content analysis of the shrimp indicates adults do not feed directly on phytoplankton, their megalope larvae do, and the majority of the adult's diet comprises benthic suspension feeders and pelagic zooplankton (Pakhomov *et al.* 1999). *Nauticaris marionis* itself forms a generous part of the diet of several land-based predators. Penguins, such as the macaroni and gentoo (*Pygoscelis papua*) (Adams *et al.* 1993), and Crozet shags (*Phalacrocorax atriceps*) (Espitalier-Noel *et al.* 1988) are all known to predate on the shrimp. *Nauticaris marionis* is also a common prey item of demersal fish (Pakhomov and Froneman, 1999) and has occasionally been found in Antarctic fur seal (*Arctocephalus gazella*) scat (Makhado *et al.* 2008). It is not an endemic species to the Prince Edward Islands, as its geographical range extends from Bouvet Island in the west to southern New Zealand in the east (Probert *et al.* 1979; Arntz *et al.* 2006). Comparatively, though *N. marionis* has been found to be much more abundant around Prince Edward Islands than other sub-Antarctic islands, and is second in total benthic biomass only to bryozoans, as recorded from dredge and photographic surveys (Perissinotto and McQuaid, 1990). It is readily found on the shallow coastal shelf around the Prince Edward Islands and on the saddle separating the two islands, with maximum abundances recorded at depths between 50 and 100 m (Branch *et al.* 1993; Perissinotto and McQuaid, 1990).

The life history of *N. marionis* was investigated by Pakhomov *et al.* (2000). They discovered the shrimp is a partially protandric hermaphrodite, with peak hatching occurring in April and May. As megalope larvae, they survive in undetected locations before moulting into juveniles and settling on the benthos eight/nine months later. Diel vertical migration continues until they reach adulthood. The majority of juveniles develop into males, and then trans-mutate into females before the reproductive season in the third year. Only a minority develop directly into females without going through the male phase, or into males without progressing to the subsequent female phase. It is proposed that this sex reversal at the Prince Edward Islands may be affected by the changing environment as it is likely that sexual differentiation occurs at an early stage (Pakhomov *et al.* 2000).

The South African Environmental Observation Network, via the Department of Environmental Affairs' annual relief voyage to the Prince Edward Islands, leads an ongoing inter-island benthic survey investigating benthic ecosystems, biodiversity and ecological functioning of the Prince Edward Islands with an emphasis on long-term change. Much is known about the biology and life history of *N. marionis*, but no information has been reported on the benthic habitat that the shrimp are associated with. With populations of penguins and seabirds declining (Crawford *et al.* 2003), understanding the ecology of an important prey species such as *N. marionis* could be important in elucidating the reasons for this. This study contributes to the ongoing research and will improve knowledge and understanding of these sub-Antarctic islands. The objective of this study was to determine if *N. marionis* distribution is associated with particular habitat types, with 'habitat' being considered as a combination of substratum and sessile epibenthic cover. The aim was to quantify *N. marionis* abundances at different depths and survey the sessile epibenthic cover around the islands, with the purpose of answering the following question:

Do depth or habitat characteristics influence densities and spatial distribution of *N. marionis*?

Based on the importance of biogenic structure and substratum characteristics to benthic species in many different systems (Coen *et al.* 1981; Lewis, 1984; Collie *et al.* 1997; Bradshaw *et al.* 2003), and high *N. marionis* densities being previously recorded at shallow depths (Branch *et al.* 1993) we propose the following hypotheses:

- 1) Higher densities of *N. marionis* will be associated with greater percentages of sessile epibenthic cover.
- 2) There will be higher densities of *N. marionis* in shallow, inshore stations in close proximity to the islands.

2. Materials and Methods

Sampling

The benthic substratum and epibenthic cover around the Prince Edward Islands were studied during the annual relief voyages of the R/V SA Agulhas II research vessel in April 2013 and 2015, as part of an ongoing assessment of the islands' marine environment. Sample stations were chosen to match those that were sampled historically by Branch *et al.*, 1993 (Figure 2). At each station, still images of the benthos were taken using a Canon 550D DSLR Camera housed on a heavy steel frame on skis, called SkiMonkey III, containing laser pointers to scale the area covered in the image, and lights to illuminate the benthos (Appendix A). The camera system was towed behind the SA Agulhas II at approximately 0.5 knots for 20 minutes, covering transects of approximately 300 m. The camera was set at a 30 degree angle relative to the horizontal plane, and still photographs were taken in quick succession, resulting in a series of non-overlapping oblique images along a transect. For reasons explained in the following paragraph, only a portion of each image was used for processing. The area of seabed processed was demarcated by a standard 50 x 50 cm digital quadrat, which, depending on the orientation of the camera, equated to real ground areas of between 0.33 - 0.46 m² in each image. To compensate for the oblique angle of the images, a system of calibration techniques were employed to calculate the area of the images processed. Firstly, in an attempt to replicate the undulation of the sea floor surface, the camera system was tilted/pitched

at varying angles on a flat surface with the backdrop of a gridded area board (Appendix B). The position of the lasers was then marked on transparent stencils for the various angles. These stencils were used to align the laser markings on each image before processing. For each image processed, the angle of the transparency stencil that matched the laser markings on the image was noted and used to calculate the specific area of the image. The images were predominantly taken during daylight hours; but because of the vessel's tight schedule two stations (M23 and M36) were sampled after sunset. Along with the time of sampling, depth was also recorded.

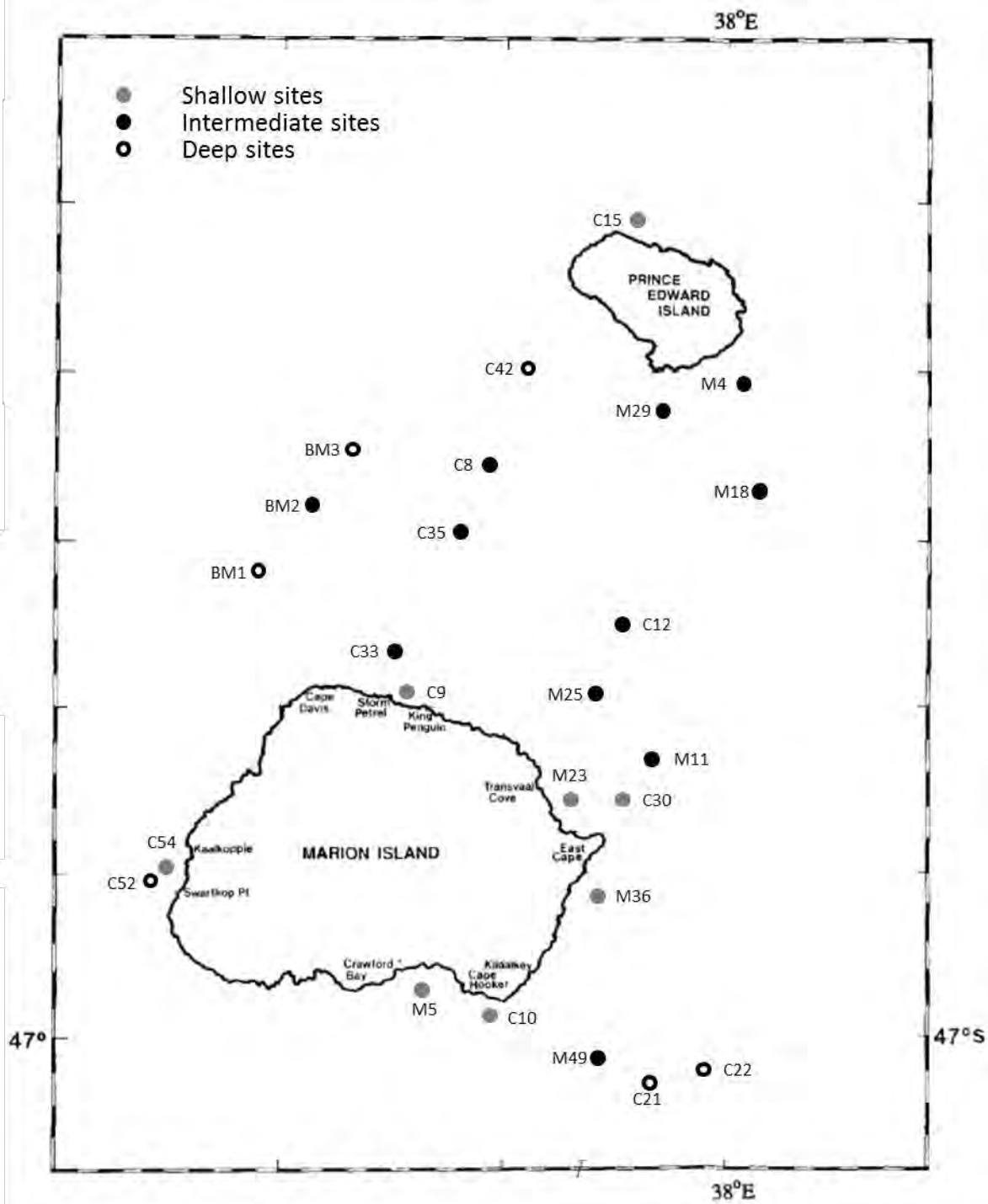


Figure 2. Map of the Prince Edward Islands and the location of stations sampled during annual relief voyages in 2013 and 2015. Adapted from Branch *et al.* 1993.

Image Processing

Twenty five high quality images from each station were selected for further processing where possible, although only 20 images were of adequate quality at stations C15, C22 and M29. The images were processed using the

software package Coral Point Count with Excel extensions (CPCe) version 4.1 which estimated the percentage cover of epibenthic structure by overlaying a point-count grid. Point counts were done using a standardised area demarcated in CPCe, thereby excluding the blurry periphery of the image where identification of epibenthos was extremely difficult (Appendix C). This ensured a high degree of certainty when identifying fauna. Only sessile epifaunal- and macro-algal organisms with 3-dimensional structure were recorded, while all mobile organisms were excluded from the percentage cover analysis. Counts of *N. marionis* were recorded for each image and their respective densities were calculated.

$$\left(\frac{\text{number of shrimp}}{\text{area of quadrat}} \right)$$

Stations were grouped according to their substratum type, being pre-defined visually as either mud, gravel, rocky-sand or rocky-mud (Appendix D). Stations were grouped into depth bins of shallow (50 – 120 m), intermediate (121 – 299 m) or deep (300 – 500 m).

Multivariate Statistical Analyses

Sessile epibenthos abundance (percentage cover) and *N. marionis* density data were analysed using PRIMER (Plymouth Routines in Multivariate Ecological Research, version 6.1.18; Clarke and Gorley, 2006) and PERMANOVA+ for PRIMER, version 1.0.8 (Anderson *et al.* 2008) to determine the influence of sessile epibenthic cover, substratum type and depth on the distribution of *N. marionis*. The data were square-root transformed to down-weight the dominance of abundant epibenthic species or bare substratum, and then used to generate a Bray–Curtis similarity matrix. Multidimensional scaling (MDS) was used to visually represent similarities in benthic community in all stations surveyed. This included plots based on raw data, and plots based on data averaged per station. Various scaled bubble plots and vectors were overlaid to highlight relevant patterns. Only vectors with a Spearman correlation measure > 0.4 were plotted. To test the two hypotheses a semi-parametric permutation analysis of variance (PERMANOVA) was used to test for significant differences in epibenthic assemblages between samples of where *N. marionis* was present and where they were absent, and among depth zones, using the similarity matrix created from square-root transformed data. A Type III sum of squares

was employed with permutation of residuals under a reduced model. “Depth bin” (fixed factor) was crossed with “*N. marionis* presence/absence” (Fixed factor). Initially a main test was performed to determine the influence of sessile epibenthic cover and depth on *N. marionis* distribution, followed by pair-wise tests where differences or interactions were significant. A SIMPER analysis was also performed to determine which sessile epibenthic assemblages were responsible for any observed differences emerging from the MDS and PERMANOVA analyses between stations hosting *N. marionis* and those that did not.

Hierarchical clustering (using Bray–Curtis coefficients) with SIMPROF routine (which identifies significantly different groupings of stations) testing station-averaged data with substratum removed from analysis was used to determine the degree of similarity of epibenthic cover among stations. Information about *N. marionis* presence/absence, as well as substratum type was overlaid to investigate if the station clusters could be matched to the patterns of *N. marionis* status or substratum type.

As a result of an unbalanced data set and non-normal data distribution, a one-way PERMANOVA was run on univariate *N. marionis* density data to test if densities of *N. marionis* were affected by different sessile epibenthic assemblage groupings (biological habitat types), as indicated by the cluster output. “Biogenic habitat” was the single fixed factor. The data were square-root transformed to down-weight the dominance of high densities, and then used to generate a Euclidean distance similarity matrix. A type III sum of squares was used, with an unrestricted permutation of raw data. A pair-wise test was then performed to test for significant differences between the biogenic habitat groupings.

The relationship between *N. marionis* density and depth was tested using a Pearson’s correlation on $\log(x+1)$ -transformed density data and untransformed depth data. The data were then plotted in a scatter plot and fitted with a linear trend line.

To test whether sampling during the day or night influenced the abundance of *N. marionis*, a one-way PERMANOVA was performed on shrimp density data with time as a single fixed factor. A subset of data was used as only two stations were sampled at night (M23 and M36). Two stations sampled during the day (C9 and M11), displaying similar epibenthic community structure as M23 and M36, as evident from the cluster analysis, and which were located adjacent to the stations sampled at night were included in the analysis. As there were only 2 stations that were sampled at night, comparing them with all the stations sampled during the day would have resulted in a heavily unbalanced design. The data were square-root transformed to down-weight the dominance of high densities, and then used to generate a Euclidean distance similarity matrix. A type III sum of squares was used, with an unrestricted permutation of raw data.

3. Results

In total, 609 images were sampled at 25 stations (8 shallow, 11 intermediate and 6 deep) for sessile epibenthic percentage cover and *N. marionis* counts. A total of 2244 *N. marionis* was identified in 144 images (24 %) from 12 stations (48 %). The depth of stations sampled ranged from 50 – 500 m. In this study *N. marionis* was found at a depth range of 62 – 160 m, in densities up to 200.m⁻². The average percentage cover of sessile epibenthos per station ranged from 5 – 97 %, with the percentage cover generally decreasing with increasing depth. Shallow stations averaged 70 % cover, intermediate stations 57 % cover, and deep stations averaged only 18 % cover.

Influence of Sessile Epibenthic Cover

Initial multivariate testing supported the hypothesis that epibenthic habitat differs significantly between stations hosting *N. marionis* and those that do not (Figure 3). Multi-dimensional scaling analysis revealed a clear

separation of sessile epibenthic data that closely matched patterns of presence/absence of the shrimp.

Epibenthic communities where *N. marionis* was found clustered more closely together, compared to those where the shrimp was not found, which were more dispersed.

Based on percentage cover data of sessile epibenthic biota, PERMANOVA analysis revealed a significant difference between stations which hosted *N. marionis* and those at which the shrimp was absent (Pseudo-F = 65.07, $P(\text{perm}) < 0.001$, d.f. = 1), and a significant interaction between *N. marionis* status and depth (Pseudo-F = 28.98, $P(\text{perm}) < 0.001$, d.f. = 1; Table 1).

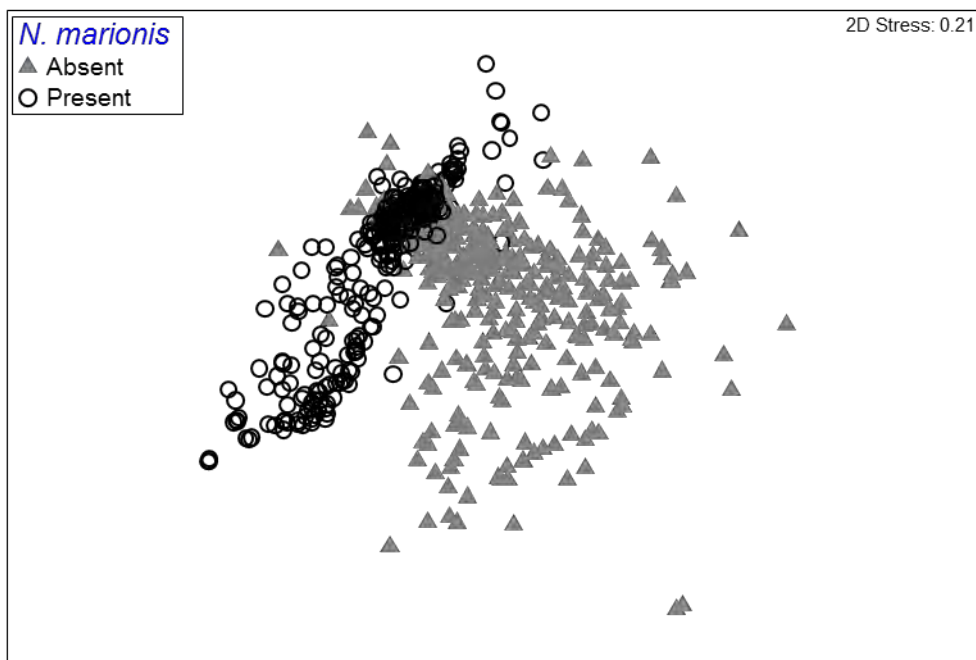


Figure 3. MDS plot representing Bray-Curtis similarity for sessile epibenthic cover data indicating samples from stations where *N. marionis* was present and stations where *N. marionis* was absent. Data points show sample-level information, but presence/absence information is demarcated at the station-level.

Table 1. Results of PERMANOVA testing differences in sessile epibenthic cover among stations where *N. marionis* was present and those where *N. marionis* was absent, across depth strata.

Main	Factor	df	SS	MS	Pseudo-F	P (perm)	Unique perms
	<i>N. marionis</i>	1	1.01E+05	1.01E+05	65.067	0.0001	9949
	Depth bin	2	1.71E+05	85375	55.046	0.0001	9932
	Interaction N x D	1	44945	44945	28.979	0.0001	9915
	Res	604	9.37E+05	1551			
	Total	608	1.36E+06				
Pairwise	N x D	Groups			t value	P (perm)	Unique perms
	<i>N. marionis</i>						
	Shallow	Yes,No			6.394	0.0001	9950
	Intermediate	Yes,No			8.519	0.0001	9946
	Deep	Yes,No				no test possible	
	Depth bin						
	No	Shallow, Intermediate			5.871	0.0001	9954
		Intermediate, deep			3.999	0.0001	9941
		Shallow, deep			6.49	0.0001	9947
	Yes	Shallow, Intermediate			10.785	0.0001	9958

Examinations of SIMPER results comparing stations which hosted *N. marionis* and stations which did not, it is evident that this difference is driven by the abundance of sessile epibenthic cover present, as well as the composition of the assemblage (Figure 4). *Nauticaris marionis* was present at stations where most of the biota making up the sessile epibenthic cover was more abundant. Bryozoans, sponges, polychaetes, hydroids, red algae and brachiopods were more abundant at stations where *N. marionis* was present, while *N. marionis* was absent at stations where anemones and cerianthids were more abundant.

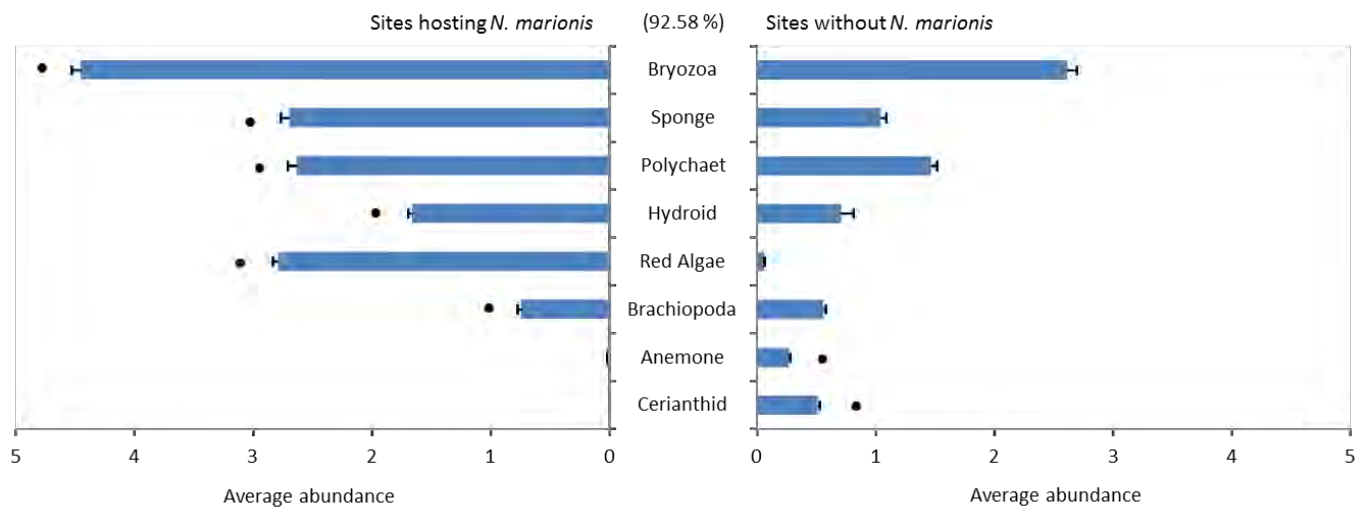


Figure 4. SIMPER results comparing average abundances (square-root transformed; + SE) of the top eight contributing sessile epibenthic biota between stations hosting *N. marionis* and stations without *N. marionis*. Dissimilarity percentage between the two groups is indicated in brackets. The group with the greater abundance per biota is indicated with a black circle.

When epibenthic cover data were averaged for each station for clarity of presentation, an MDS revealed discrete clustering of *N. marionis* present and *N. marionis* absent stations (Figure 5).

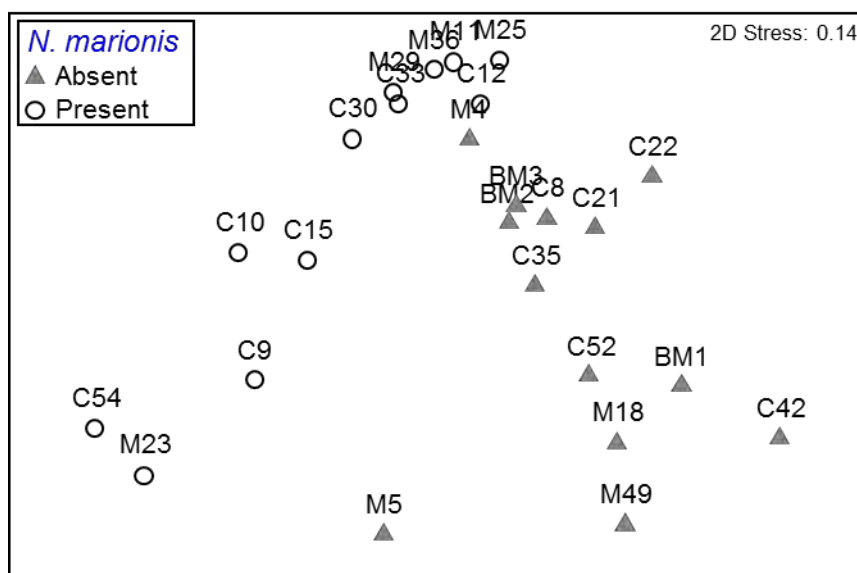


Figure 5. MDS plot representing Bray-Curtis similarity for sessile epibenthic cover data comparing stations hosting *N. marionis* and those without *N. marionis*, for averaged data per station.

Results of the SIMPROF cluster analysis grouped stations into four significantly different groups, based on their averaged sessile epibenthic assemblage data (Figure 6). These groupings represent biogenic habitat types, and are further referred to as biogenic habitat Group 1 - 4. When overlaid with information of *N. marionis* presence/absence, it is evident that these groupings predominantly reflect the sessile epibenthic conditions that create suitable or unsuitable biogenic habitat for *N. marionis*. Both biogenic habitat 'Group 2' and 'Group 3' did not host any *N. marionis*, while 'Group 1' and 'Group 4' mostly consist of stations where the shrimp is present. However, both Groups 1 and 4 contain a single '*N. marionis* absent' station each. SIMPROF analysis indicated that in Group 1, the single station without any *N. marionis* (M5) is the most dissimilar, though not significantly different, to the rest of the stations within the group (approximately 40% similar to the other stations), all of which host *N. marionis*. Interestingly though, in Group 4, the single station without *N. marionis* (M4) is not the most dissimilar to the rest of the stations (approximately 65% similar to M25 and approximately 75% similar to the other stations) which contain shrimp.

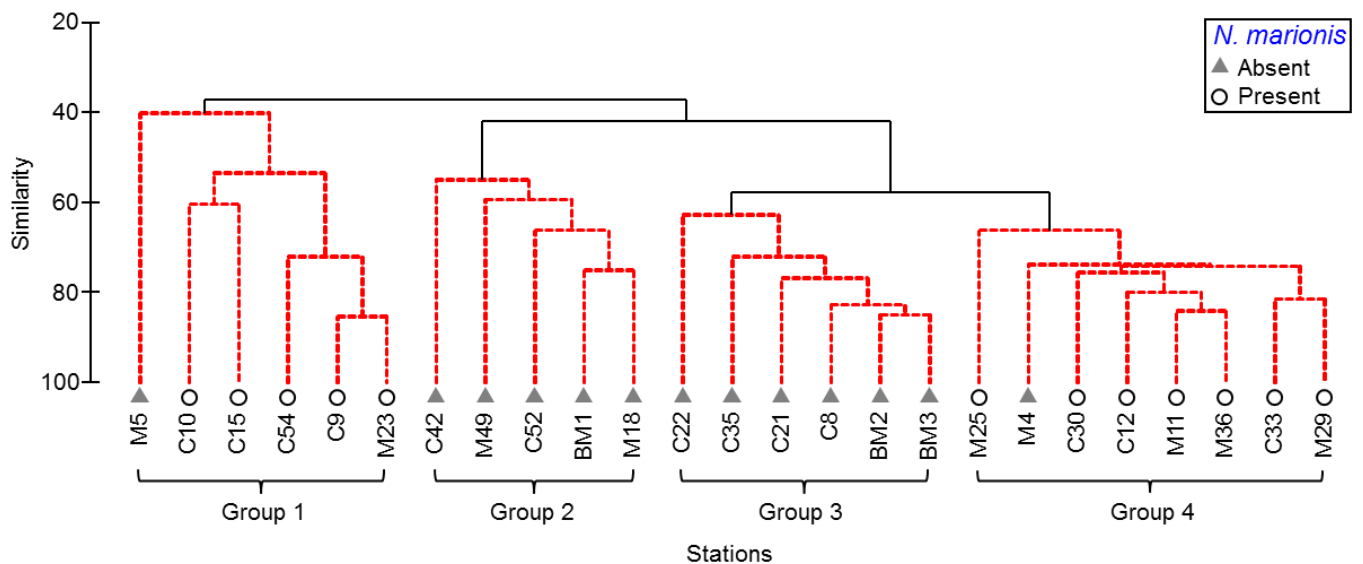


Figure 6. Dendrogram with SIMPROF derived from cluster analysis displaying the significantly different groupings of stations, based on averaged percentage cover data. Stations divided into those where *N. marionis* was present (circles), and those where *N. marionis* was absent (triangles).

A SIMPER dissimilarity analysis revealed which elements of the biota recorded were responsible for driving the differences in epibenthic community among the biogenic habitat groups (Figure 7). Group 1 (stations most dissimilar to the other groups at 38 % similarity) was characterised by the high abundance of red algae, while bryozoans were dominant in all other groups.

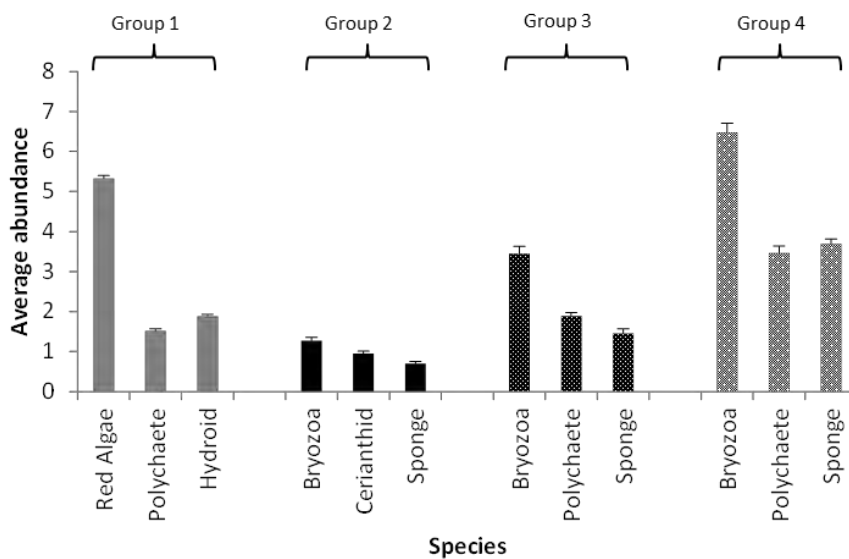


Figure 7. Bar graph of the average abundance (square-root transformed; + SE) of the top 3 biota contributing to the dissimilarity between the biogenic habitat groups, as obtained from cluster analysis. Data derived from SIMPER dissimilarity analysis.

Bryozoan abundance was considerably greater in Group 4 (*N. marionis* present) than in Groups 2 or 3 (*N. marionis* absent). There were also other differences in epibenthos abundance between the two groups where *N. marionis* was found (Figure 8). Sponge, polychaetes and brachiopods were more abundant in Group 4 (bryozoan dominated) than in Group 1 (red algae dominated).

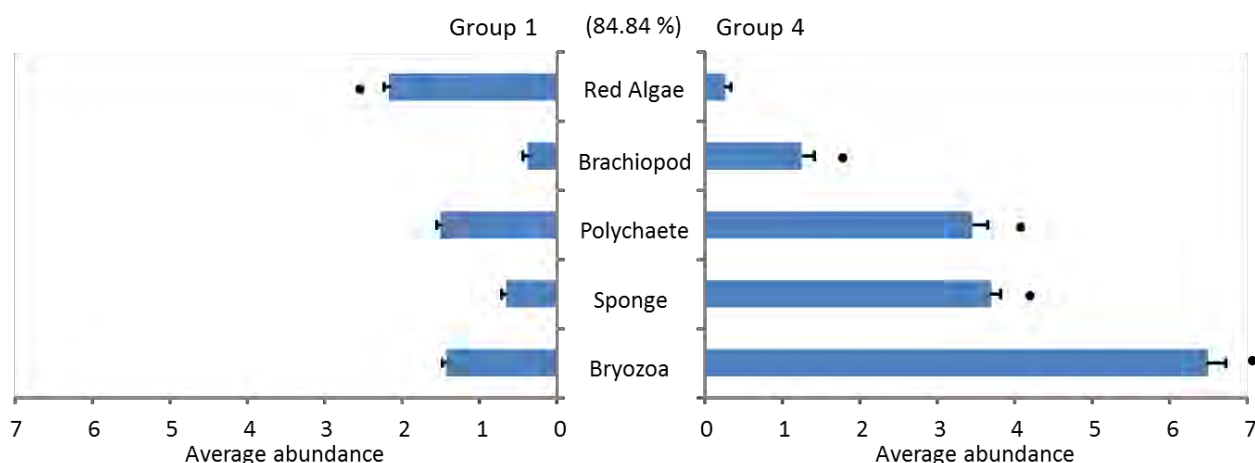


Figure 8. Comparison of average abundance (square-root transformed; + SE) of sessile epibenthic biota between biogenic habitat Groups 1 and 4. Data derived from SIMPER dissimilarity analysis. Dissimilarity percentage between the two groups is indicated in brackets. The group with the greater abundance per biota is indicated with a black circle.

The results of the second PERMANOVA tests examining the effect of sessile epibenthic cover of the different biogenic habitat groups on the density of *N. marionis* revealed significant differences among groups (Pseudo-F = 90.55, $P(\text{perm}) < 0.001$, d.f. = 3; Table 2). A pair-wise test revealed a significant difference in *N. marionis* density between the two groups containing stations where *N. marionis* was present ($t = 3.60$, $P(\text{perm}) < 0.001$; Figure 9).

Table 2. PERMANOVA results testing the effect of biogenic habitat groupings on the density of *N. marionis*.

Main	Factor	df	SS	MS	Pseudo-F	P (perm)	Unique perms
	Bio habitat grps	3	1229.9	409.98	90.554	0.0001	9949
	Res	605	2739.1	4.5275			
	Total	608	3969				
Pairwise	Bio habitat grps	Groups			t value	P (perm)	Unique Perms
		4, 3			8.8883	0.0001	9836
		4, 2			8.2798	0.0001	9832
		4, 1			3.5978	0.0007	9822
		3, 1			15.901	0.0001	9847
		2, 1			14.811	0.0001	9845

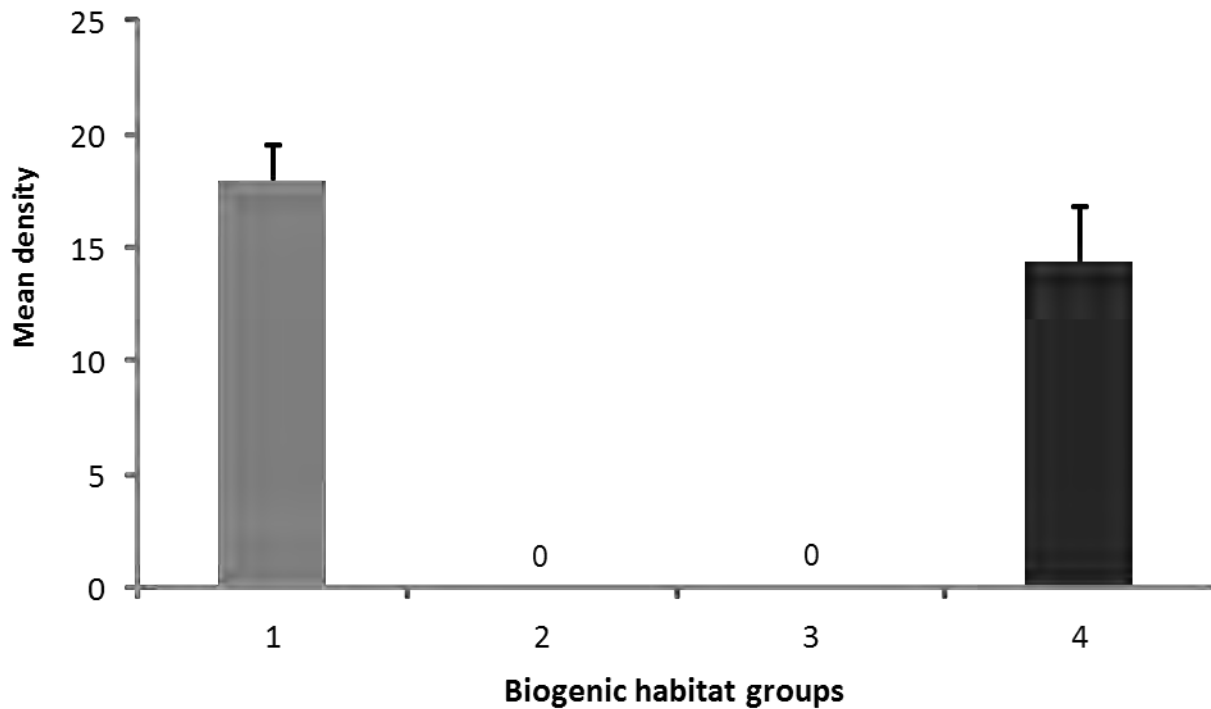


Figure 9. Mean densities ($\text{m}^2 + \text{SE}$) of *N. marionis* among the different biogenic habitat groups (based on SIMPROF data). All pair-wise comparisons among groups highly significant ($p < 0.001$).

By overlaying epibenthic cover data with bubble plots representing the percentage bare substratum, MDS illustrated that *N. marionis* seems to be associated more with stations with more cover, rather than stations with a particular substratum (Figure 10). Stations hosting shrimp had relatively low percentages of bare substratum (mean = 17.6 %, sd = 12.5), although there was one station with 49.7 % bare substratum. Stations where shrimp were not found generally had high percentages of bare substratum (mean = 76.5 %, sd = 20.5). While over 60 % of the seabed was bare substratum at most of these stations, it only accounted for 15.3 % at station M4.

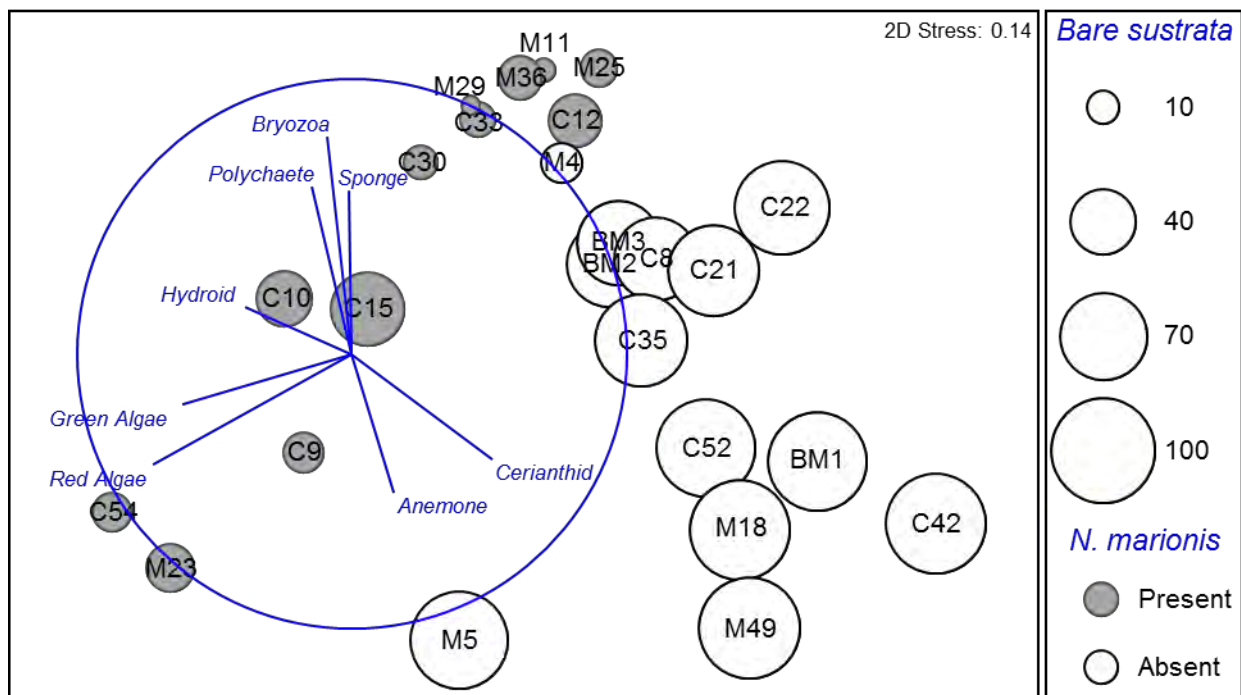


Figure 10. Bubble plot representing Bray-Curtis similarity for averaged sessile epibenthic cover data, with sessile epibenthic biota vector overlay. Bubble size represents the percentage bare substrata at each station, while white bubbles indicate stations where *N. marionis* was absent and grey indicate stations where *N. marionis* was present.

Influence of Substratum Type

Initial investigations of the influence of substratum type on the distribution of *N. marionis* revealed a high degree of overlap of the sessile epibenthic data across substratum types (not shown). When substratum type information was overlaid onto the dendrogram, it revealed that biogenic habitat groups contained stations with a mix of substratum types (Figure 11). Group 4 was the most homogenous, containing seven stations with muddy substrata, and only one gravelly substratum station (M4). Group 1 also contained two stations with muddy substrata, but the majority (four) of the stations in Group 1 had gravelly substrata. Groups 2 and 3 were very mixed, each containing three out of the four substratum types. Stations with a muddy substratum appear in all four biogenic habitat groups, while stations with a gravelly substratum were present in three out of the four groups. *Nauticaris marionis* was found at stations classified with both muddy and gravelly substrata, but the shrimps were not present at all stations with a muddy substratum, nor were they present at all stations with a gravelly substratum. No shrimp were found at stations with rocky mud or rocky sand substrata.

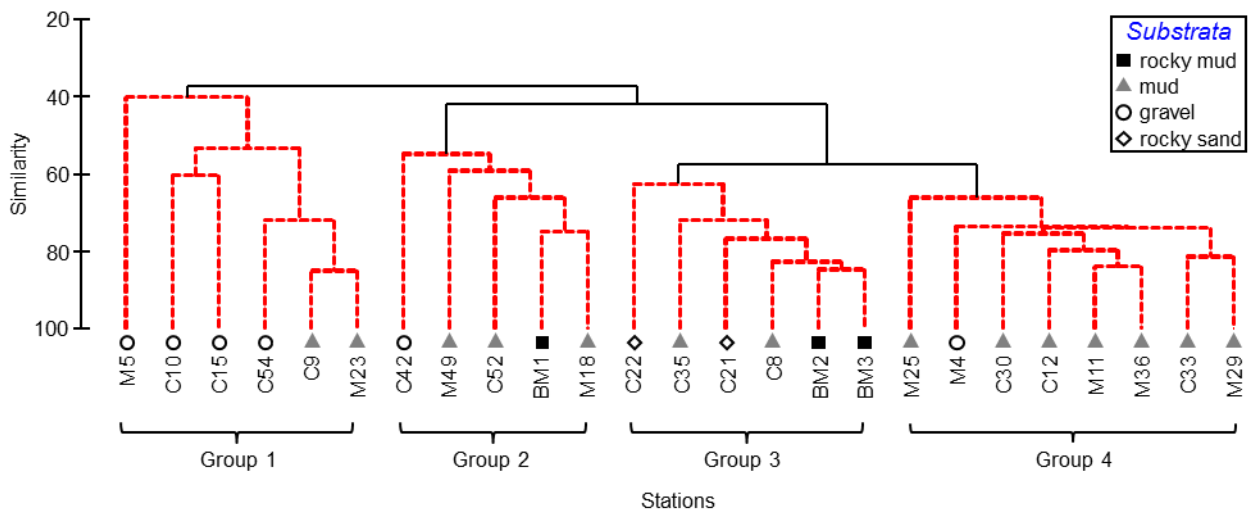


Figure 11. Dendrogram with SIMPROF derived from cluster analysis displaying the significantly different groupings of stations, based on averaged percentage cover data. Stations are further categorised with their respective substratum types.

Influence of depth

Initial investigation of the influence of depth on the sessile epibenthic community through MDS revealed some clustering separation among shallow, intermediate and deep stations (Figure 12).

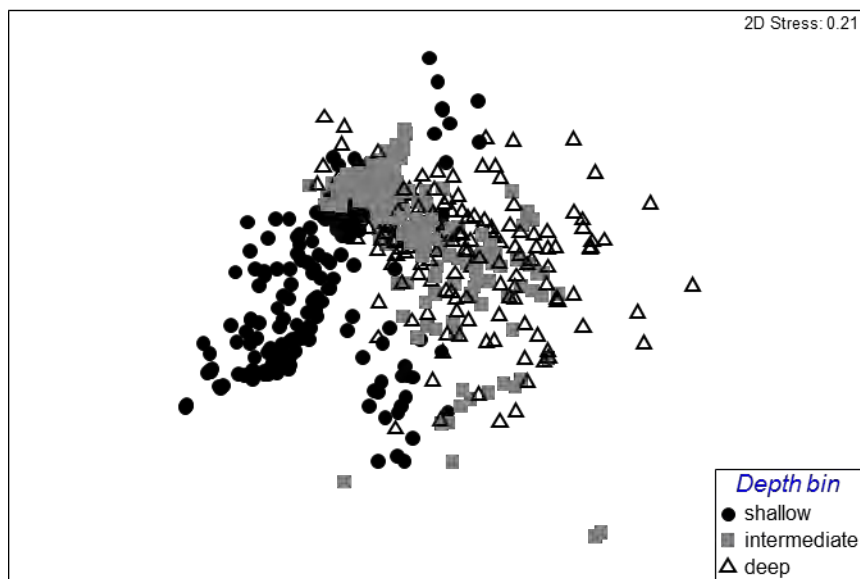


Figure 12. MDS plot representing Bray-Curtis similarity for sessile epibenthic cover data comparing replicates of stations within shallow, intermediate and deep depth zones.

The majority of shallow stations were clustered close together, however, there was overlap between shallow and intermediate stations, between intermediate and deep stations, and minor overlap between shallow and deep stations. Shallow, intermediate and deep stations displayed an increasing gradient in dispersion. The difference in epibenthic cover among the depth zones was found to be significant (Pseudo-F =55.05, P(perm) < 0.001, d.f. = 2; Table 1). An MDS plot based on station-averaged epibenthic cover data with a bubble plot overlay scaled to represent the depth at each station illustrates the influence of depth on the sessile epibenthic community (Figure 13). *Nauticaris marionis* was found in shallow and intermediate stations, but not at any deep stations. The deepest station where they were found was at 160 m. Of all the shallow stations sampled, the only one where shrimp were not found was station M5.

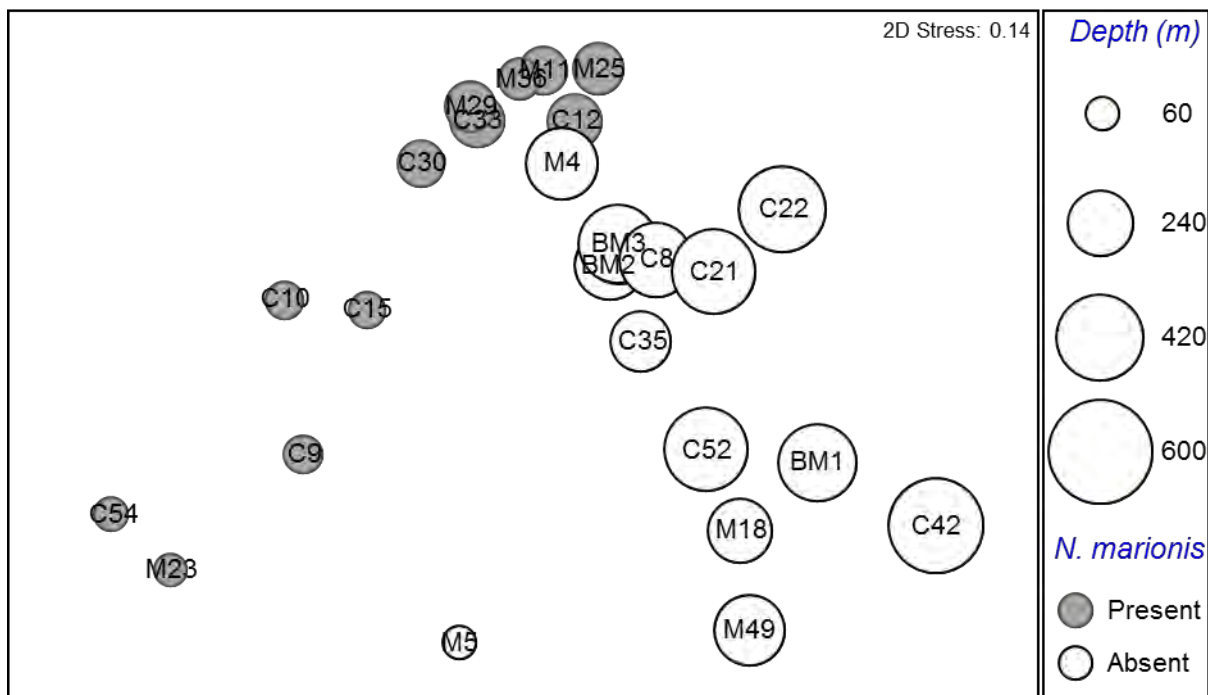


Figure 13. Bubble plot representing Bray-Curtis similarity for averaged sessile epibenthic cover data. Bubble size is related to the depth of each station, while white bubbles indicate stations where *N. marionis* was absent and grey indicate stations where *N. marionis* was present.

The dissimilarity in sessile epibenthic biota between shallow and intermediate stations was predominantly driven by higher abundances of red algae in shallow stations, and higher abundances of bryozoans, sponges and

polychaetes at intermediate stations (Figure 14a). Higher abundances of bryozoans, polychaetes and sponges in intermediate stations, and slightly higher abundances of cerianthids and gorgonians at deep stations were largely responsible for the difference detected between these two depth zones (Figure 14b). The dissimilarity between shallow and deep stations was predominately driven by higher abundances of bryozoans, hydroids, polychaetes and sponges at shallow stations, and slightly higher abundances of cerianthids and gorgonians at deeper stations (Figure 14c).

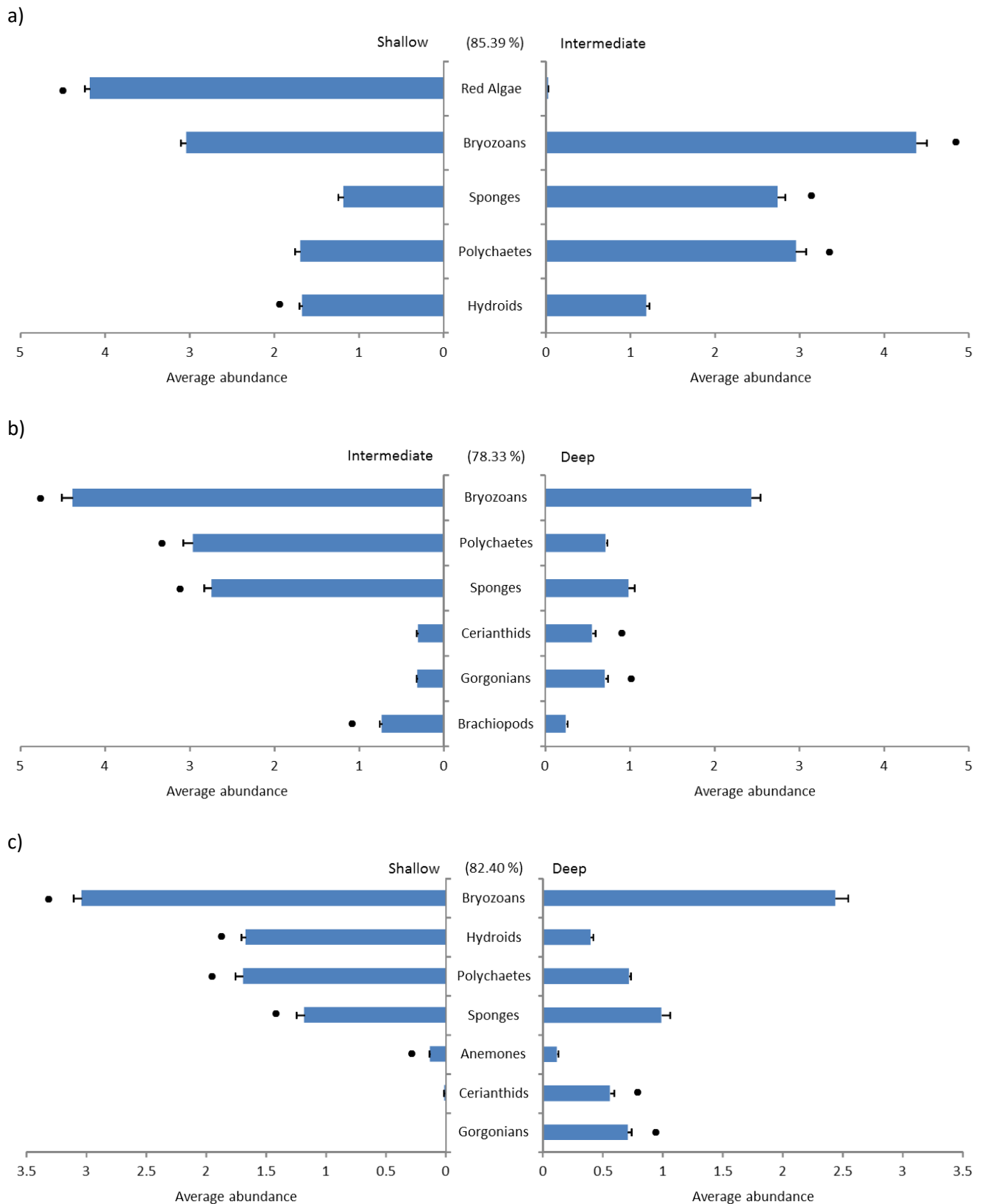


Figure 14. Average abundances (square-root transformed; + SE) of biota driving dissimilarity between a) shallow and intermediate zones, b) intermediate and deep zones, and c) shallow and deep zones. Data based on SIMPER routine. Species are arranged in descending order of contribution. Dissimilarity percentages between depths are indicated in brackets. The depth zone with a greater abundance of a given taxon is indicated with a black circle.

The Pearson's correlation showed a significant negative linear relationship existed between depth and transformed densities of *N. marionis* ($r_{23} = -0.69$, $p < 0.01$). Although shrimp were found at stations ranging from 50 – 160 m, the highest densities were found at a depth of 90 m (Figure 15).

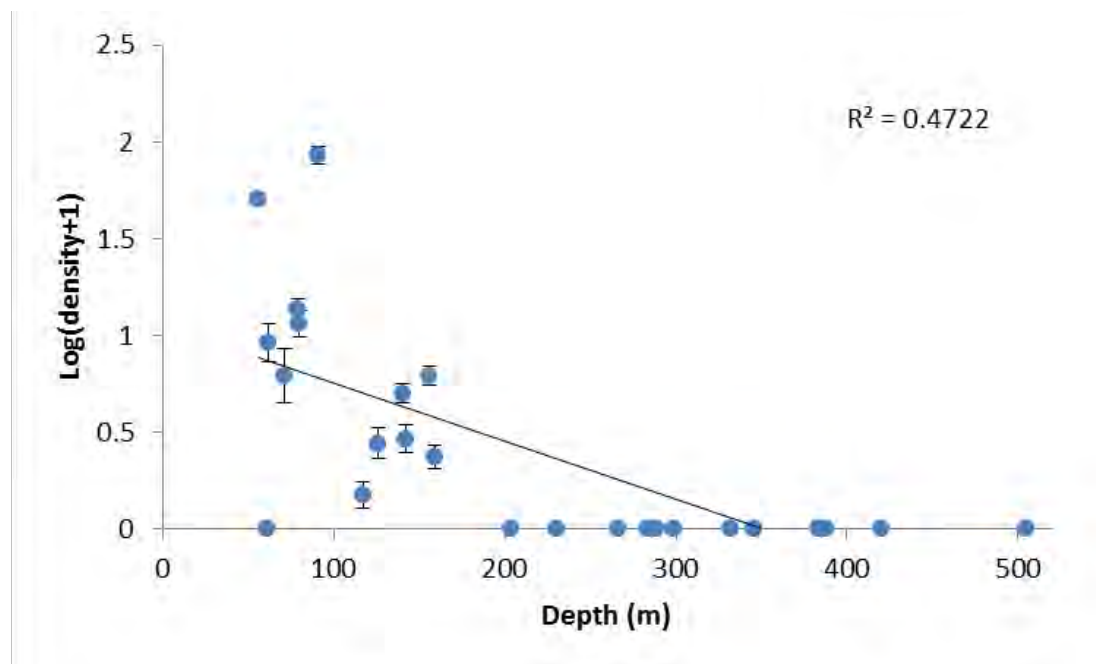


Figure 15. Scatter plot of station-averaged data displaying log-transformed *N. marionis* densities (+ SE) at different depths, including trend line with a linear fit.

Day vs Night

A single factor PERMANOVA analysis confirmed a significant difference between the densities of *N. marionis* at stations sampled during the day and comparable stations (as determined by percentage similarity in cluster analysis) sampled at night (Pseudo-F = 257, $P(\text{perm}) < 0.001$, d.f. = 1; Table 3).

Table 3. PERMANOVA results testing the effect of time of sampling on *N. marionis* density (i.e. Day vs night).

Factor	df	SS	MS	Pseudo-F	P(perm)	Unique perms
Time	1	876.56	876.56	257	0.0001	9854
Res	98	334.25	3.4107			
Total	99	1210.8				

4. Discussion

Nauticaris marionis is highly abundant around the Sub-Antarctic Prince Edward Islands and occupy an important trophic position in the ecosystem by making the enhanced primary productivity around the islands available for marine predators based on land (Perissinotto and McQuaid, 1990). Much is known about the biology, life history and ecological role of the shrimp, but not much attention has focused on its habitat requirements. This study sought to explore the distribution patterns of *N. marionis* by using a modern, non-destructive technique to sample the sessile epibenthos of the islands.

Does sessile epibenthic cover influence Nauticaris marionis distribution?

The distribution of *N. marionis* was shown to be associated with specific habitat types and specific sessile epibenthic assemblages (Figure 4). This implies that extensive changes in sessile epibenthic assemblages can lead to changes in *N. marionis* abundance around the Prince Edward Islands. Two significantly different habitat types emerged that support populations of *N. marionis* (Figure 6) around the islands. The first habitat type (Group 1, Figure 6) is made up of shallow, inshore stations (56 – 80 m) located close to the islands. All the stations making up this group were dominated by red algae, with polychaetes and hydroids contributing less to the percentage cover. This was similar to findings of Branch *et al.* (1993), who reported similar taxonomic

assemblages and an abundance of *N. marionis* ($\bar{x} = 24.2^{-2}$, $SE = 6.8$) at shallow, inshore stations. *Nauticaris marionis* densities were significantly higher in these stations dominated by red algae when compared to the stations in Group 4 (Figure 9). However, it must be noted that *N. marionis* densities at stations in Group 1 may be under-represented as it was difficult to identify the predominately red-coloured shrimp against the backdrop of red algae. If anything, absolute densities of *N. marionis* may be even higher than recorded at these stations. The second habitat type (Group 4, figure 6) was mostly made up of stations located offshore on the saddle between the islands (Figure 2) where dominant epibenthic species were bryozoan filter feeders, with sponges and polychaetes also being abundant. Similar findings were reported by Perissinotto and McQuaid (1990), who described *N. marionis* being second in overall biomass only to bryozoans around the islands, and by Branch *et al.* (1993) who described the soft-sediment substratum of the inter-island plateau to be covered by bryozoans, sponges and polychaetes. The maximum mean shrimp density in this study reached over $90.m^{-2}$, at a depth of 90 m at station M36. This was higher than the maximum estimates of both Perissinotto and McQuaid (1990), and Branch *et al.* (1993) who reported densities as high as $80.m^{-2}$ and $49.m^{-2}$ respectively, at depths below 100 m. Improved photographic technology could have played a role in this, with high definition digital imagery assisting in the ease of shrimp identification. The shrimp at the majority of the stations in Group 4 (bryozoan dominated) were less richly pigmented (pers. obs), possibly as a consequence of the lack of red algae found at these stations. As *N. marionis* is an opportunistic consumer, feeding indiscriminately on food sources around them, their pigmentation could possibly be influenced by carotenoids found in prey they feed on. Alternatively, they could be actively changing their colouration to better match their background in order to minimize the threat of predation.

Sessile epibenthic structures provide these shrimp with complex habitat that may reduce their chances of conspicuous detection by visual predators (Collie *et al.* 1997) in a manner similar to that of seagrass meadows providing shelter to other shrimp species (Coen *et al.* 1981; Lewis 1984). Different assemblages of sessile epibenthos may afford the shrimp different degrees of shelter, as has been reported for other aquatic

invertebrates (Reed *et al.* 2004). Naturally, dense covers of sessile epibenthos will provide greater protection from predators than sparse cover (Shervette *et al.* 2011). This reflects the patterns detected in my study, as *N. marionis* was found at stations with an abundance of epibenthic cover and lower percentages of bare substratum.

Does substratum type influence Nauticaris marionis distribution?

My results indicate that substratum type on its own is not a good determinant of the sessile epibenthos community that will colonise it, nor does it consistently affect the abundance of sessile epibenthos (Figure 11). Although the effect of substratum type on sessile epibenthic community was not explicitly tested in this study, substratum type appears to be less influential on the benthos than previously reported where substratum types were deemed to be very important in shaping epibenthic communities (Craig and Jones, 1966; Albrecht, 1998; Sahade *et al.* 2004; Katsanevakis *et al.* 2007). Substratum type alone, therefore, seems not to have a direct influence on the distribution of *N. marionis*. Rather, it is a combination of substratum type, the species composition of sessile epibenthic cover, and the extent of biogenic cover which appears to influence *N. marionis* distribution. As stated previously, the primary habitat type that *N. marionis* is associated with (Group 1, Figure 11) is made up of inshore stations (56 – 80 m) located close to the islands. Even though these stations contained very similar sessile epibenthic compositions, the substratum supporting these communities was not homogenous. Most (66.6 %) of these stations have a gravelly substratum, but there are also two stations with a muddy substratum. The same can be said of the second habitat type that *N. marionis* is associated with (Group 4, figure 11), which is mostly made up of stations located offshore on the saddle between the islands. The stations in this group predominately have muddy substrata, except for one (again, station M4). As no shrimp were found at station M4, while they were found at the other stations in the group, suggests that a difference in substratum or some other unmeasured factor(s) is likely the underlying reason for shrimp not occurring at station M4. However, similar to the stations in Group 1 that were found to host *N. marionis*, station M4 had a gravelly substratum. The notion that substratum type plays a dominant role in influencing shrimp distribution is

further questioned upon closer inspection of the two remaining groups (Groups 2 and 3, Figure 11). Neither of these groups contained stations at which *N. marionis* was found. Although no shrimp were found at stations with either a rocky-mud substratum or a rocky-sand substratum, shrimp were found at stations with a muddy and gravelly substratum. Both Group 2 and Group 3 contained at least two stations that had either a muddy or a gravelly substratum.

It seems as if it is not so much a case of substratum type, but how much of the substratum is covered with biogenic forming epibenthic species which influences the distribution of *N. marionis*. The abiotic factors, such as particle size or ground firmness, which determine substratum type may play a role in determining the infauna or epibenthos able to inhabit, but this does not mean they dictate the carrying capacity of the substratum, or the extent to which it is covered (McNulty et al, 1962; Driscoll, 1967; Osman, 1977). The more the substratum is covered, the more structural habitat is provided, which increases the abundance and biodiversity of biotic fauna (Coen et al. 1981; Lewis, 1984; Bradshaw et al, 2003).

Does depth influence Nauticaris marionis distribution?

The results of this study reveal that depth did have a significant influence on the distribution of *N. marionis*. *Nauticaris marionis* was not found deeper than 160 m, even though it has previously been described inhabiting depths up to 775 m (Perissinotto and McQuaid, 1990) and 690 m (Branch et al. 1993). While range shifts are known in the Antarctic (Allan et al. 2013), the discrepancies in depth ranges among studies may also be a result of artefacts related to the sampling equipment used. For example, benthic dredges are able to collect hidden animals while cameras are not. The negative correlation between depth and *N. marionis* densities detected in this study, suggests that higher densities of shrimp are found at shallower depths. As depth increases shrimp density decreases. Depth not only influenced the epibenthic assemblages, but also the amount of sessile epibenthic cover observed. However, depth and sessile epibenthic cover are not independent of each other,

therefore, it is difficult to apportion the relative influence of each. Red and green algae rely on sunlight for food production, so they are restricted to the relatively shallow depths of the euphotic zone (Brody and Emerson, 1959; Moreira *et al.* 2000). Depth may influence the distribution of *N. marionis* through associated changes in epibenthic cover. Generally, as depth increased the epibenthic assemblages shifted from highly abundant (shallow stations) to sparsely covering the substratum (intermediate stations) to predominately bare substrata (deep stations). This would explain why *N. marionis* was found at shallow stations and some intermediate stations, but not at deep stations. The only shallow station where no shrimp were found was at station M5. However, sessile epibenthic cover was scarce at this station and therefore did not provide much habitat for the shrimp.

Does time of sampling influence density of Nauticaris marionis?

The results of day vs night comparisons indicated that time of sampling did influence *N. marionis* densities on the sea floor. This suggests that the estimates of *N. marionis* abundance from the stations sampled during the day are likely to be an underrepresentation of their actual abundances. However, because only two stations were sampled at night compared to two comparable day-sampled stations, the significant differences in shrimp densities in the day-night comparison may not be due to time of sampling alone. Sampling and analysis is needed to further interrogate the effect of sampling time on *N. marionis* density. *Nauticaris marionis* is known to form a suprabenthic layer which extends 5 – 10 m above the seabed (Perissinotto and McQuaid, 1990), but it is not known if this is a diurnal movement or a short-term feeding tactic, as this shrimp is predominately a bottom dweller. While the megalope larvae of *N. marionis* exhibit diurnal diel migration, moving up the water column to feed at night (Perissinotto and McQuaid, 1990), this has not been noted for juveniles or adults. As larvae display downward movement during daylight to avoid visual predators, it would seem counter-intuitive if juveniles and adults formed a suprabenthic layer above the seabed during the daytime. Yet, results from this study suggest that if time of sampling does in fact influence shrimp abundances on the seabed, then theoretically, they should be found in greater abundances on the seabed during the daytime, where they would

have more protection from predators. At station 36 (one of the stations sampled at night), shrimp-like organisms can be seen in the water column about 1 m above the seabed in the images, but because they are not in the camera's focus, it is not certain whether they are *N. marionis* or another shrimp species. Assuming that they are indeed *N. marionis*, this could mean that the density estimates for this station would be even higher than previously stated. However, as diel migration is an adaptive predator-avoidance tactic, it can be employed as a predator-specific response with organisms generally moving up the water column at night, although downward movements to the sea floor are also known to occur (Carey *et al.* 2011).

Conclusions

Nauticaris marionis was found to associate with higher abundances of sessile epibenthic organisms which create three-dimensional biogenic structure and increase habitat complexity. Red algae and bryozoans were particularly important epibenthic groups driving the presence of *N. marionis*. Although substratum type seemed to influence the sessile epibenthic community, it was not considered to be the primary driver in determining the distribution of *N. marionis* in this study. Suitable epibenthic habitat decreased with depth, as did shrimp density. There is some evidence that time of sampling (day or night) influences densities of *N. marionis* on the seafloor, however, further research is necessary for more conclusive findings. In general, results suggest that *N. marionis* populations are strongly linked to structure forming epibenthic organisms, and that changes to these fauna and flora may have consequences for the distribution and abundance of the shrimp. Such relationships may have potential impacts on predators that rely on *N. marionis* for a significant portion of their diet.

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Appendix

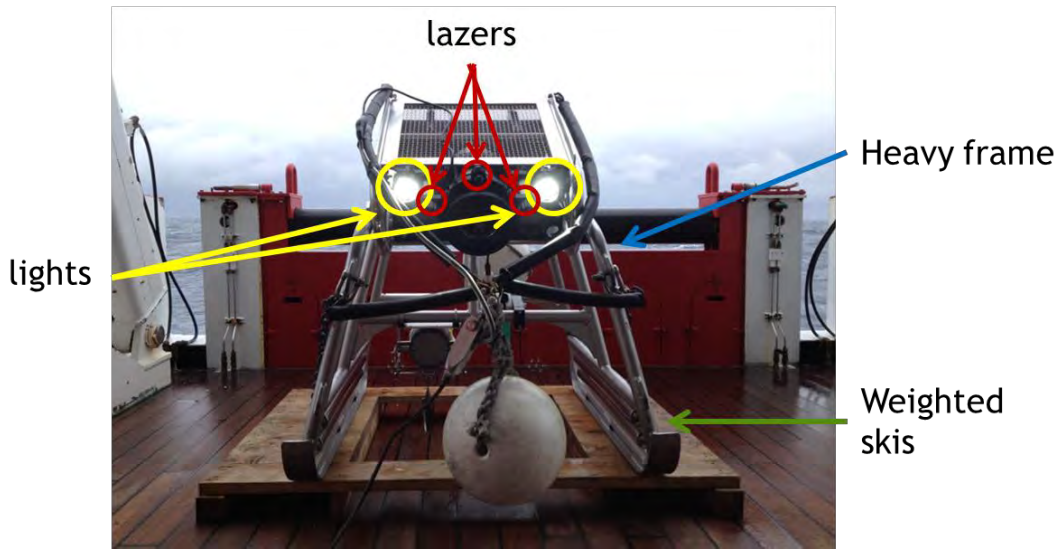


Figure A. The towed camera apparatus, SkiMonkey III

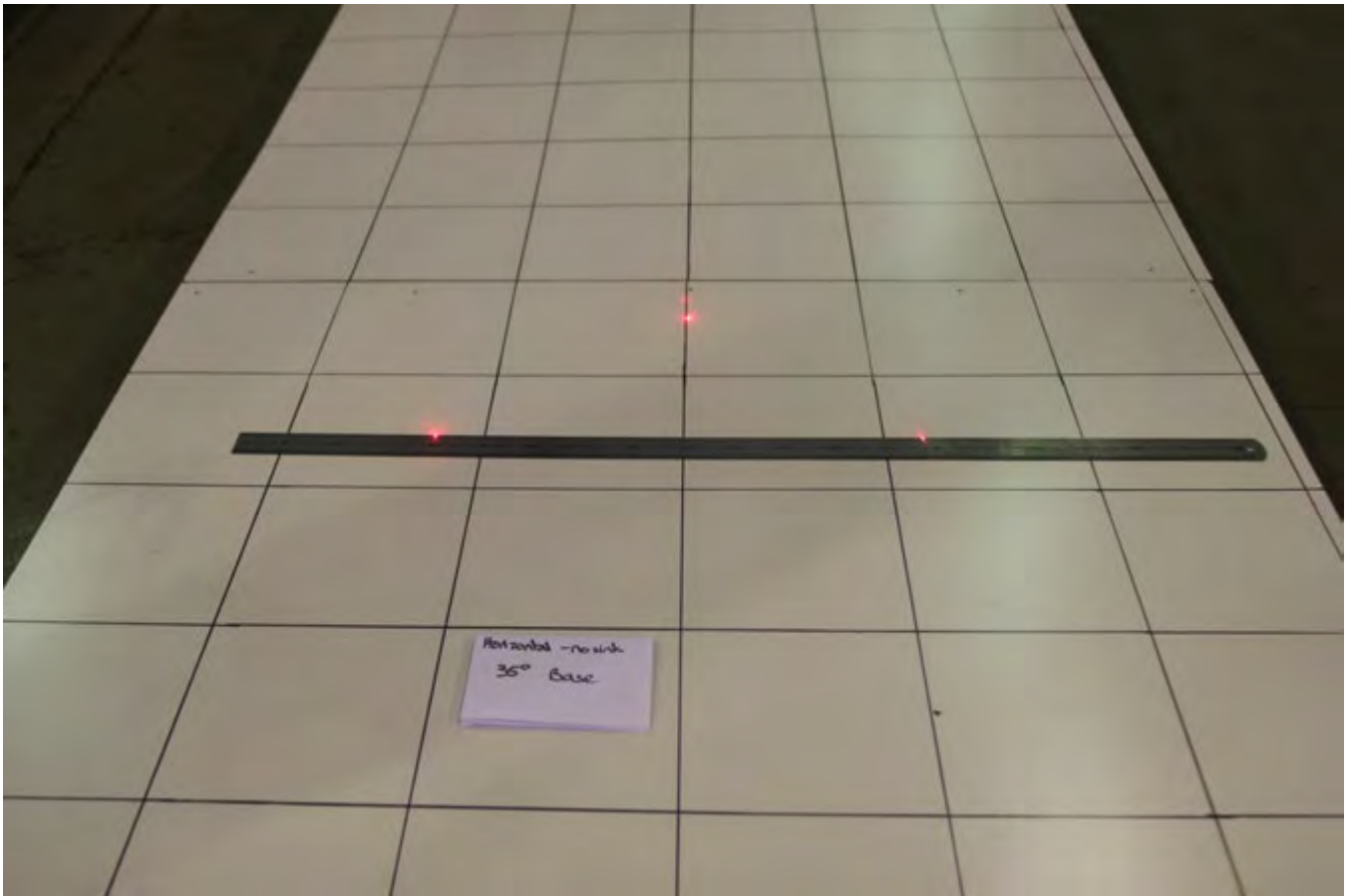


Figure B. Gridded board used to calculate the area processed using the position of the lasers.

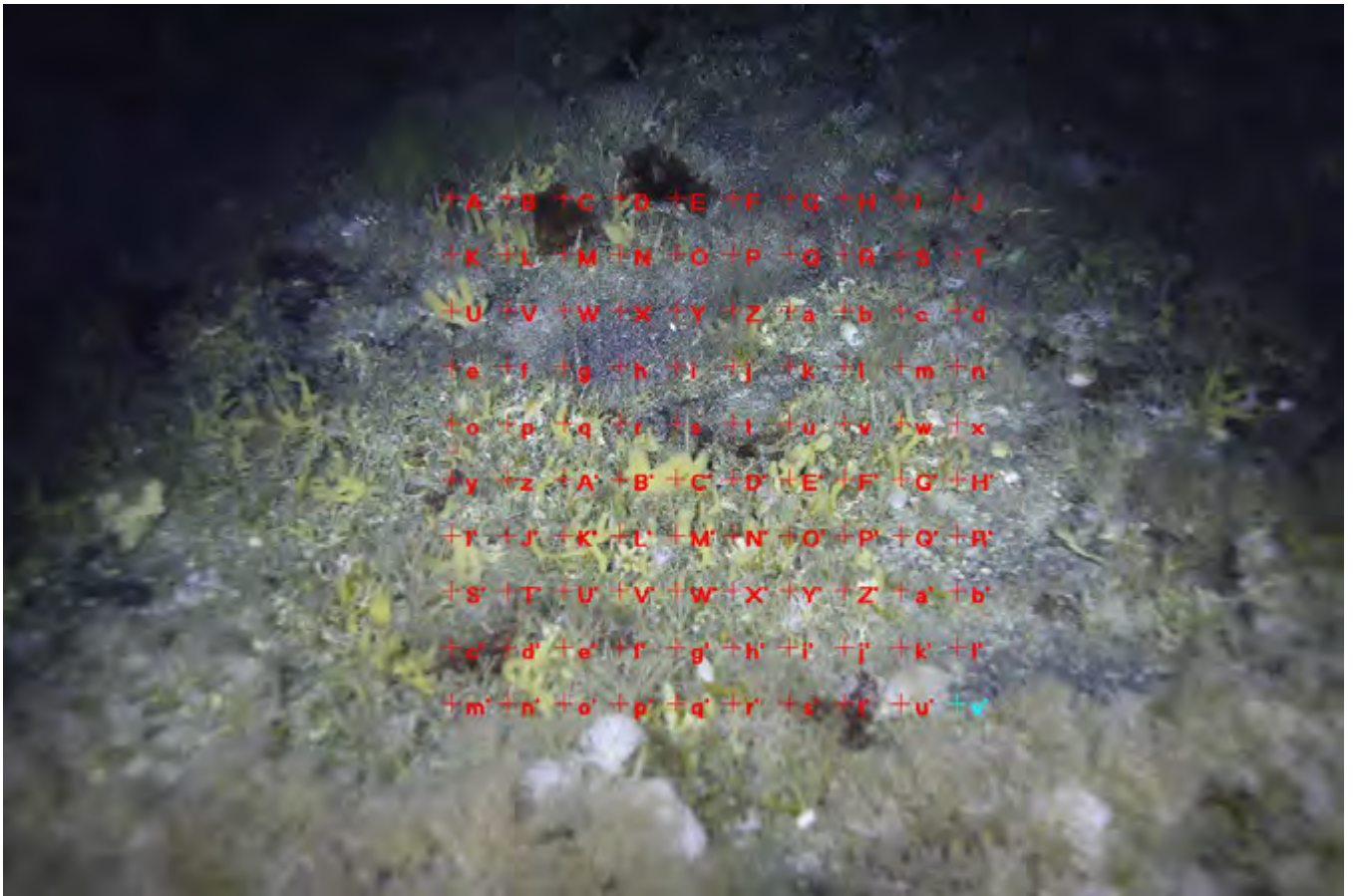


Figure C. Example of image processed in CPGe with a point-count grid overlay.

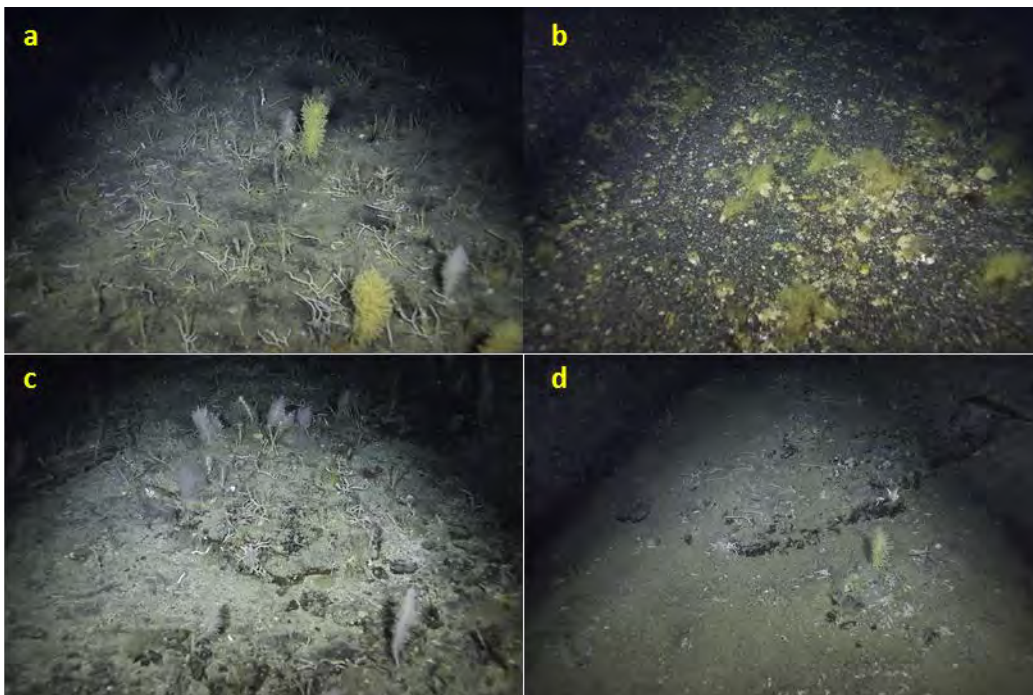


Figure D. Images of substratum type: a) mud, b) gravel, c) rocky mud and d) rocky sand.